Berkeley, Washington State College, Rocky Mountain Herbarium, Philadelphia Academy of Sciences, Missouri Botanical Garden, United States National Herbarium, New York Botanical Garden, and Gray Herbarium. We are greatly indebted to the curators of these herbaria. We are also indebted to Prof. Carl Epling for assistance with the Latin diagnoses. Many of the chromosome determinations were made while the senior author was a National Research Council Fellow in residence at the John Innes Horticultural Institution, Merton (now at Bayfordbury) England.

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RELICT ISLANDS OF XERIC FLORA WEST OF THE CASCADE MOUNTAINS IN OREGON

LeRoy E. Detling

A student of the Pacific Northwest flora frequently has his attention called to the occasional occurrence west of the Cascade crest of plant species whose normal range is in the more arid regions of the Rogue River Basin to the southward, or the basins and plateaus east of the Cascades. Closer investigation reveals some rather significant features in the distribution of some of these outliers—features which may have a bearing upon the study of the origins and past migrations of the Northwest flora.

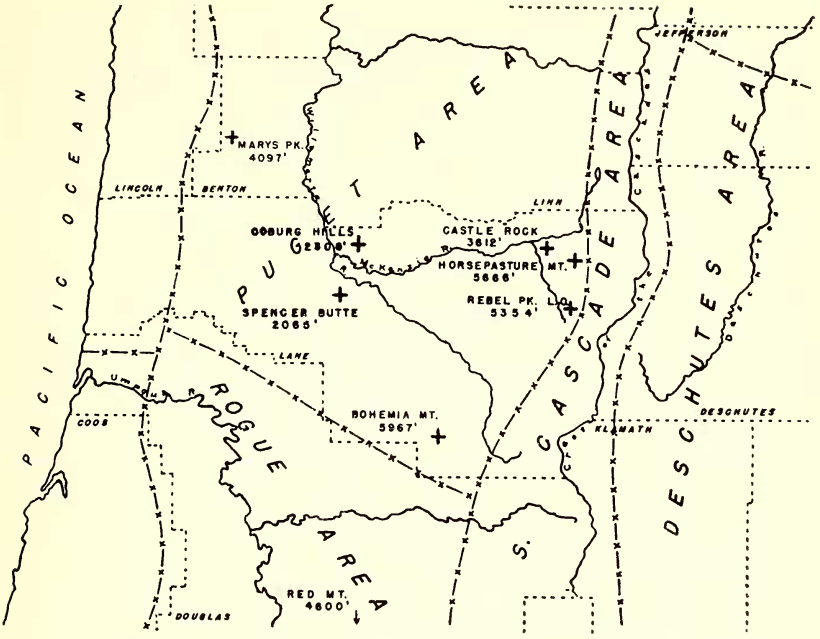
In the first place, the stations where any one of the species is found are not scattered indiscriminately over the region west of the mountains. On the contrary, they are relatively few in number and in each station several to many of the outlier species are concentrated within a restricted area. In the second place, these restricted areas are in all cases mountain summits where a special set of environmental conditions obtains, producing a habitat differing considerably from that immediately surrounding it, and similar in many respects to those found

in the Rogue River Valley or the regions east of the Cascades. In other words, these summits constitute isolated "islands" of xeric flora within a general mesic region.

The writer has made a study of eight of these islands (see accompanying map and table of xeric species), and the results and conclusions are presented herewith. Field studies, which have included all these islands, have been supplemented by herbarium study at the University of Oregon and Oregon State College. Collections made by Rayma Brown on Spencer Butte, Roy Andrews on Horsepasture Mountain, and J. Rollo Patterson and Wm. H. Baker (1951) in the Bohemia-Fairview district were of great value.

With one exception all these islands are located along the west slopes of the Cascade Mountains in Lane and Douglas counties, Oregon. The exception, Marys Peak, is in the heart of the Oregon Coast Range in Benton County. All but Red Mountain are included in that vegetation area which we have designated as the Puget (to be explained in a later paragraph). The latter is in the northern part of the Rogue Area. The general region is one of moderate to excessive annual precipitation, most of which falls during the winter, and of moderate summer and winter temperatures. Elevations of the peaks range from about 2000 feet on Spencer Butte, near Eugene, to nearly 6000 feet in the Bohemia-Fairview district. The most easterly of the islands is the one on Horsepasture Mountain, which is about twenty miles in a straight line from the nearest ponderosa pine forests of eastern Oregon. These twenty miles, however, include the unbroken belt of subalpine vegetation along the crest of the Cascades.

In each case the peak is composed of a mass of igneous rock which has been eroded away to form an isolated point or short ridge. As erosion has progressed, the soil originating from the rock at the summit has largely been washed down the slope, leaving a mass of rock either completely exposed or covered over with a thin layer of soil. There is no indication that the surrounding forest trees or deep-rooted shrubs have ever been able to invade these places. The shallow soil is subject to rapid drainage, and the vegetation is exposed to the dessicating action of sun and wind. Temperatures are undoubtedly affected by heat absorption by the dark rocks and by the protection afforded by crevices and rock ledges. One significant effect of this would probably be the lengthening of the growing season for those plants established in this situation. It is under these conditions of moisture and temperature and without serious competition with the surrounding species that we find the xeric flora which we are discussing. The mountain slopes below the islands are in all instances covered with moderately dense forest. Below 4500 feet this forest is made up of Douglas fir (*Pseudotsuga taxifolia*) with its associated



vine maple (*Acer circinatum*), Oregon grape (*Berberis nervosa*), and salal (*Gaultheria Shallon*). Above this elevation it is mixed with, or even replaced by, such types as noble fir (*Abies procera*), subalpine fir (*A. lasiocarpa*), western white pine (*Pinus monticola*), and mountain hemlock (*Tsuga Mertensiana*). For the sake of comparison it is of interest to note that as yet no xeric species have been found to occur on the summit of Hardesty Mountain, a peak within this area which reaches an elevation of 4250 feet. In this case, for some reason, a moderately deep soil cover has been retained at the summit, allowing a dense growth of *Pseudotsuga, Castanopsis,* and *Rhododendron* to become established there.

From the results of several seasons' collecting on the eight floral islands we have selected thirty-two species whose normal distribution is in the more arid vegetation areas to the south or east. Undoubtedly the list would be extended by more thorough collecting on the same peaks as well as by the inclusion of other peaks of similar environmental conditions in the same general region. The accompanying table indicates the occurrence of the species on the islands under consideration. Considerable variation is apparent in the number occurring in any one island. Of particular interest is Rebel Peak, in the watershed of the South Fork of the McKenzie River, where no less than eighteen xeric species are either directly associated with, or among rocks in the immediate vicinity of a patch of *Arte-*

misia tridentata, the only occurrence of this sagebrush known to the writer from west of the Cascade Mountains.

The isolated character of the several islands gives evidence of their being relicts of a former widespread xeric flora. It is generally conceded by students of plant distribution that such islands are left in favorable niches in the wake of retreating or shrinking populations. An advancing population, on the other hand, presents a relatively continuous front, and is not preceded to any great distance by outliers of its species.

The chief significance of our xeric islands lies in their relation to the floras of the four or five vegetation areas which are in closest proximity to them, and particularly to the three among this number in which the relict species have their normal range today. For the purpose of this discussion these areas will be referred to by the names adopted by the writer in a previous study (Detling, 1948). The first is the Rogue Area, comprising roughly the valleys of the Rogue and Umpqua rivers. The second area, the Deschutes, includes the plateau and basin region east of the Cascades and south of the Ochoco and Blue Mountains, extending to Klamath and Summer lakes, and to the northeastern corner of Nevada. The Columbia Area takes in, in a general way, the valleys of the middle Columbia River and its main tributaries in north central Oregon and south central Washington. The Puget Area is made up of the valleys of the Willamette-Puget Trough, and extends from the Rogue Area northward to southwestern British Columbia. Finally, the higher elevations of the Cascade Mountains between the Columbia and Klamath rivers comprise the South Cascade Area.

The xeric flora alluded to was presumably at one time the basic flora of the Puget Area, including the west slopes of the Cascades up to an elevation of nearly 6000 feet, probably the highest altitude at which the relicts now occur. Since the relicts in their normal range are largely associates of the ponderosa pine forests, we must assume that at the time the xeric flora occupied the Puget Area the latter had a climate comparable to that which now obtains in the Rogue, Deschutes, and Columbia areas, where continuous stands of this pine are now extant. Annual precipitation would have ranged from twelve to forty-five inches (less than half that of the present period); January mean temperatures must have ranged between 26° F. and 40° F., while July mean temperatures were probably from 60° F. to 73° F. Evidence of such a warm-dry cycle in the Pacific Northwest, culminating about six to eight thousand years ago, is offered by the bog-pollen studies of Hansen (1947). According to these studies the warm, dry climate probably persisted in this area until as late as about four thousand years ago. It seems quite possible, therefore, that a xeric flora such as is today associated with the ponderosa pines was the dominant

feature of the west slopes of the Cascades as recently as that. Hansen (op. cit.) finds no evidence of any increase of this species in the Willamette Valley during the post-glacial dry period, and he suggests the possibility that the scattered stands now found in the southern end of the valley may be the result of a more recent invasion. In any case, it is difficult to explain the absence of ponderosa pine today above the level of the valley floor in the Puget Area other than by supposing that competition with other forest types has eliminated it completely from the deeper soils, while at the same time, due to its deep-rooted habit, it has never been able to persist on the rocky, shallow soils of the mountain summits and ridges.

Returning to the present distribution of the plant species in the relict islands, we find that each falls into one of six distinct patterns. These patterns may be summarized in the following manner, each group of species having its normal distribution in the area or areas indicated in the appropriate heading:

I. Rogue. *Erigeron foliosus confinis, Hieracium cynoglossoides nudicaule, Sidalcea asprella, Viola Sheltonii.*

II. Deschutes. *Arenaria formosa, Bromus polyanthus, Lupinus lepidus medius.*

III. Rogue-Deschutes. *Collomia linearis, Delphinium depauperatum, Eriogonum umbellatum, Madia minima.*

IV. Rogue-Columbia. *Eriogonum compositum pilicaule, Sisyrinchium Douglasii.*

V. Rogue-Deschutes-Columbia. *Arabis Holboellii retrofracta, Claytonia lanceolata, Crocidium multicaule, Erythronium grandiflorum pallidum, Gilia aggregata, Hackelia diffusa, Linum Lewisii, Lupinus laxiflorus, Microsteris humilis, Phacelia linearis, Poa scabrella, Prunus emarginata, Sanicula graveolens, Sedum Douglasii.*

VI. Deschutes-Columbia. *Arnica Parryi, Artemisia tridentata, Polygonum Douglasii, Silene Douglasii.*

None of the thirty-two species under consideration has its normal distribution in the Columbia Area alone.

In a previous paper (Detling, op. cit.) the writer has emphasized the point that the important feature of any vegetation area is not its boundaries, which are vague under the best of conditions, but rather its "environmental center," the point about which are grouped the extremes of environmental factors which produce the optimum conditions for the plant species inhabiting the area. Since in the last analysis the positions of these environmental centers are determined by the physiography of a region, it is highly probable that they have been relatively fixed for many thousands of years. If the climate of the Pacific Northwest were to shift toward a warm-dry maximum, the environmental extremes in such areas as the Rogue and Deschutes would become intensified, their influence would

spread progressively from the center outward, and their floras would advance at the expense of those areas, like the South Cascade, with a cool-moist combination of extremes. The reverse movement would occur as the climate became again cooler and more humid.

The South Cascade Area, with its marked extremes of moisture and low temperatures is interposed between the Deschutes and Puget areas in such a way as to hinder if not actually prevent any interchange of floral elements between these two until what was probably the culmination of a warm-dry cycle. Minimum elevations of the Cascade crest in this region are approximately 5000 feet, with most of the ridges rising at least 1000 or 1500 feet above this. A xeric Puget flora would have reached the elevation of all but the very highest of what are now the relict islands before contact would be made with a similar xeric flora east of the crest.

No such intervening area is interposed between the Rogue and the Puget, and the boundary separating the two is relatively indefinite. With a general increase in dryness and warmth, it is reasonable to suppose that a xeric flora advancing from the Rogue would reach the west slopes of the central Oregon Cascades before a similar xeric flora would cross the crest of the range from the Deschutes, and therefore that a large part of this element as it occurs in the Puget Area migrated in from the south.

What appears to be strong evidence in support of this theory is the distribution of those species in groups I and IV above, comprising about 18 per cent of the total xeric flora. These are Rogue species which are either restricted to that area except for the outliers in the Puget islands, or have an additional center of distribution in the Columbia Area, but in either case are absent from the Deschutes. A striking example of the latter type of distribution is that of *Eriogonum compositum*. The typical variety of this species with glabrous stems and peduncles is found commonly east of the Cascades except in a portion of the Columbia Area. The variety *pilicaule*, with pubescent stems and peduncles, replaces this in the Rogue and in the Columbia Area just eastward of the Columbia Gorge, and is the only form found on the Puget islands, where it occurs with considerable frequency.

A somewhat similar distribution pattern is presented by Garry oak (*Quercus Garryana*). This species extends northward from the central valley of California through the valleys of the Rogue and Puget areas to Vancouver Island and the lower Fraser River. An arm of its range extends through the Columbia River Gorge and eastward along the middle Columbia River and its tributaries. So far, it has not been reported as occurring east of the Cascades between the lower Deschutes River Valley and the Klamath River. In the Puget Area it is

largely restricted to the drier, lower elevations of the broad valleys, although it does occur on two or three of the xeric islands.

Several other species have this same distribution, e.g., *Dentaria tenella* var. *pulcherrima,* which is very abundant in the Rogue River Valley, fairly common in Hood River, Wasco, and Klickitat counties, and is found at rare stations in the Puget Area, including the Bohemia-Fairview island.

While this *Quercus* and *Dentaria* type of distribution does involve parts of the Puget Area other than the islands, and consequently ought perhaps to be considered as a special case, nevertheless it is of interest in this discussion in that it does emphasize the close relationship between the Rogue and Columbia areas, and the fact that this relationship does not necessarily involve the Deschutes Area at all.

An interesting species whose distribution pattern does not coincide with any of those cited above is *Allium crenulatum.* It occurs on three of our xeric islands, on Saddle Mountain in Clatsop County, Oregon, and in the Olympic Mountains of western Washington. According to Dr. Marion Ownbey (unpublished correspondence), its closest affinity seems to be with *A. parvum,* a species occurring east of the Cascades, and is part of a complex of xeric species having its center of dispersal to the south of our area.

While it seems reasonable that the earlier immigrants of the ponderosa pine flora reached the Puget Area from the south, when the upper limits of this flora reached the level of the Cascade crest under the influence of the extreme dryness and warmth, there probably was an influx of additional species from the east. This may have been the pathway of many of those relicts whose present normal distribution does not include the Rogue Area. Whether any of these species were ever present in the Rogue is problematical. The floras of the Rogue River Valley and the Klamath Basin have a great many species in common today, and there is no reason to doubt that at one time there may have been more of these, which have since disappeared from one or the other of the areas.

Where the various elements of the xeric flora came from in the first place is not within the scope of the present paper. Those which did not originate in the massif of the Siskiyou Mountains seem to have reached its eastern valleys and plateaus from the lower slopes of the Sierra Nevada or the central valley of California. From this point some of the species apparently continued northward on the east side of the Cascades, while others migrated westward to the valleys and canyons of the Siskiyou Mountains and thence to the Rogue River, possibly by way of the gap north of the Shasta Valley. Why they may have taken these divergent pathways is a subject for future investigation.

TABLE 1. DISTRIBUTION OF XERIC SPECIES AMONG THE RELICT ISLANDS

Xeric species	Red Mountain	Bohemia-Fairview	Rebel Peak Lookout	Horsepasture Mountain	Castle Rock	Spencer Butte	Coburg Hills	Marys Peak
Allium crenulatum		x					x	x
Arabis Holboellii retrofracta	x							
Arenaria formosa		x	x					
Arnica Parryi			x	x				
Artemisia tridentata			x					
Bromus polyanthus		x	x					
Claytonia lanceolata		x						
Collomia linearis			x					
Crocidium multicaule						x	x	
Delphinium depauperatum	x	x						
Erigeron foliosus confinis		x			x			
Eriogonum compositum pilicaule		x	x	x	x			
Eriogonum umbellatum		x	x	x				x
Erythronium grandiflorum pallidum	x	x						x
Gilia aggregata		x	x	x				
Hackelia diffusa			x					
Hieracium cynoglossoides nudicaule		x						
Linum Lewisii		x	x					
Lupinus laxiflorus			x	x		x	x	
Lupinus lepidus medius		x						
Madia minima					x			
Microsteris humilis		x	x					
Phacelia linearis						x	x	
Poa scabrella						x	x	
Polygonum Douglasii		x	x	x		x		
Prunus emarginata		x	x					
Sanicula graveolens		x	x	x				
Sedum Douglasii		x	x	x		x		
Sidalcea asprella							x	
Silene Douglasii			x	x				x
Sisyrinchium Douglasii						x		
Viola Sheltonii		x				x	x	

SUMMARY

Distribution patterns of thirty-two xeric plant species occurring on isolated mountain tops west of the Cascade Mountains of Oregon suggest that they are relicts of a once widespread xeric flora which originated, first, in the Rogue River Valley, and secondly, on the plateaus of east-central Oregon.

They have persisted on the mountain summits because of the arid and relatively warm conditions of the shallow soil and exposed dark rocks, and the consequent freedom from competition with the surrounding mesic forest types.

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Fig. 1. Location of islands of xeric flora in central western Oregon.

BALSAMORHIZA TEREBINTHACEA AND OTHER HYBRID BALSAM-ROOTS

William A. Weber

Balsamorhiza terebinthacea (Hook.) Nutt. was one of the earliest described taxa in the genus *Balsamorhiza.* It first appeared in the literature as *Heliopsis* (?) *terebinthacea* Hooker ([1834] 1840) and was described in the same article with the type species, *Balsamorhiza Hookeri,* which Hooker called *Heliopsis* (?) *balsamorhiza.* The taxon has been accepted as a species by most subsequent authors, including Peck (1941), Rydberg (1917), St. John (1937), and by the monographer of the genus, Ward M. Sharp (1935).

Hooker's diagnosis was as follows (the italics by the present author):

> H.? terebinthacea: pubescens, foliis radicalibus *petiolatis–ovato-lanceolatis sinuato–pinnatifidis crenato–serratis,* involucri foliolis numerosis lanceolato–acuminatis imbricatis caulem paucifoliatum subaequantibus, radice crassa balsamifera. Hab. Common at Fort Vancouver, on the Columbia, and in the grounds of the interior. Douglas.—*Closely allied to the preceding species* [H. balsamorhiza], and yielding in its root the same terebinthine juice.

In studies on natural hybridization in the genus *Balsamorhiza,* Ownbey and Weber (1943) showed that intersectional crosses between species of the Section *Eubalsamorhiza,* with pinnatifid leaves, and the Section *Artorhiza,* with triangular-cordate leaves, result in introgressants which tend to preserve the habit and leaf-size of the *Artorhiza* parent while they pick up various degrees of the lobing of the *Eubalsamorhiza* parent. Thus, a large number of intermediate individuals occur which have the general leaf outline of the *Artorhiza* species, but which possess leaf-margins varying from a few scattered crenate teeth all the way to deeply and irregularly pinnatifid. In taxonomic practice, these individuals have been called *Balsamorhiza terebinthacea.*